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STUDIES ON OAT BREEDING. II—SELECTION WITHIN PURE LINES

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BULLETIN 235.

STUDIES ON OAT BREEDING. II. SELECTION WITHIN PURE LINES.[1]

By Frank M. Surface and Raymond Pearl.

Previous to 1910 it was almost universally assumed that small fluctuating variations were, to some extent at least, inherited. It was further believed that such variations were cumulative in effect and that substantial progress in breeding in a desired direction could be made by selecting, in successive generations, those individuals showing the given character in the most pronounced fashion. Since the appearance of de Vries's Mutation Theory and the great impetus given to genetic studies by the rediscovery of Mendel's Law this conception of the process of inheritance has been materially changed.

De Vries produced a large amount of experimental evidence tending to show that there are two sharply defined classes of variation. The one called fluctuating or continuous variation (*Modifikation* of the Germans) is due entirely to differences in the environmental influences. These variations, caused by external conditions, he believed were not transmitted, in any degree, from one generation to the next. The second class called discontinuous variations, mutations, etc., have their origin in variations in the germinal substance. These variations *are* transmitted from generation to generation. The distinction, then, is between variations which arise in the germ plasm and hence are inherited and variations which arise in the soma and are not inherited. This distinction was pointed out years before by Weismann on purely theoretical grounds.

Mendelian results in countless experiments with various plants and animals have shown that individual characters are inherited

[1]Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 79.

as units. It is clear that there is something in the germ cell that is transmitted in its entirety and apparently unchanged from one generation to the next. When organisms with two opposing (allelomorphic) characters are crossed, each of these characters is recovered in the second generation and each will breed true in subsequent generations. Apparently such characters are essentially unchanged by having gone through the cross.

Hence the present conception of the germ plasm is *not* that of a plastic substance which can be moulded by the environment or by selection but rather that of a mosaic made up of a vast number of definite, stable units, each perfectly fitting into its appropriate place. The hereditary process can be altered only by changing or interchanging one or more of these units. Interchange of units can be easily affected by hybridization. How experimentally to affect one of these units is one of the great problems of modern biology.

The ordinary fluctuating variations due to changes in environment in no way influence these independent units (factors or genes) of the germ plasm and hence are not inherited. Only changes which affect these germ plasm units can be transmitted to the following generation.

So much for the modern conception of the hereditary process. It is clear that if this theory of inheritance is the true one, the selection of fluctuating (somatic) variations will not influence the characteristics of the offspring.

In 1903 Johannsen[2] announced that in self-fertilized plants there was no effect of selection within a "pure line." He defined a "pure line" as the offspring of a single, self-fertilized, homozygotic individual. In such a line all of the individuals would possess exactly the same germinal constitution. Hence except for the fluctuations caused by external conditions every individual would be like every other individual. Johannsen supported his theory by a large amount of experimental evidence from beans.

This experimental result harmonized so well with the conception of the germ plasm outlined above and derived from other sources that it readily gained credence among biologists. Since

[2]Johannsen, W. Ueber Erblichkeit in Populationen und in reinen Linien. Jena, 1903, pp. 68.

the appearance of Johannsen's work numerous other investigators have studied the same problem in other organisms. In 1908 Jennings[3] published his results on the selection within pure lines of paramecium. In this extensive work he was able fully to confirm Johannsen's results. Tower[4] selected for intensity of color in chrysomelid beetles for 12 generations without obtaining any permanent result. East and Hayes[5] found that selection to increase the number of leaves on self-fertilized tobacco plants gave no results. Hutcheson[6] has recently shown that thirteen years of selection to increase the yield of pure lines of wheat have resulted in no increase. Von Rümker[7] and his students have also pointed out that seven years of selection in pure lines of wheat have not changed the characters studied.

These and many other investigations along similar lines have tended to confirm Johannsen's theory and even to extend it to the results of cross-fertilization between individuals homozygous for the factors in question.[8]

On the other hand Castle[9] in a number of recent papers has taken exception to the pure line theory. He maintains that selection *is* able to change the unit characters or factors. As

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[3]Jennings, H. S. Heredity, Variation and Evolution in Protozoa, II. Proc. Amer. Phil. Soc., Vol. XLVII, No. 190, pp. 393-546, 1908.

[4]Tower, W. L. An Investigation of Evolution in Chrysomelid Beetles of the Genus Leptinotarsa. Carnegie Institution of Washington Publication No. 48, pp. 320, 1906.

[5]East, E. M. and Hayes, H. K. A Genetic Analysis of the Changes Produced by Selection in Experiments with Tobacco. Amer. Nat., Vol. XLVIII, pp. 5-48, 1914.

[6]Hutcheson, T. B. Thirteen years of Wheat Selection. Amer. Nat., Vol. XLVIII, pp. 459-466.

[7]V. Rümker, K., Lerdner, R. und Alexandrowitsch, J. Die Anwendung einer neuer Methode zur Sorten und Linienprüfung bei Getreide. Zeit. f. Pflanzenzucht. Bd. 2, pp. 189-232, 1914.

[8]Cf. Pearl, R. The Inheritance of Fecundity in the Domestic Fowl. Amer. Nat., Vol. XLV, pp. 321-345, 1911. Also The Mode of Inheritance of Fecundity in the Domestic Fowl. Jour. Exper. Zoöl., Vol. 13, pp. 153-268, 1912.

[9]Castle, W. E. The Inconsistency of Unit Characters. Amer. Nat., Vol. XLVI, pp. 352-363, 1912.

———— and Phillips. Piebald Rats and Selection. Carnegie Institution of Washington Publication No. 195, 1914.

———— Pure Lines and Selection. Journ. of Heredity, Vol. 5, pp. 93-97, 1914.

evidence he submits the results of six years (13 generations) of breeding hooded rats. Attempts were made both to increase and to decrease the hooded pattern. He was able to do both of these things and then by return selections to bring the character back to its original condition.

This work is open to the criticism that his rats may not have been homozygous for all the factors concerned in the pattern determination. The stock with which he started was derived from pedigreed animals used by MacCurdy in a Mendelian study of coat color.[10] If, as is implied in the text, these animals were extracted recessives from Mendelian crosses it is quite possible that they were heterozygous in respect to many characters. Castle maintains that the hooded pattern is a simple unit character and hence if the rats breed true to this they must be homozygous. However, it is entirely possible that there are various modifying factors closely associated with the hooded pattern for which the animals were not homozygous. Indeed the work of MacCurdy and Castle shows some evidence of this in that "the hooded pattern, when extracted from a cross with wild stock, shows a different variability, the pigmentation of the extracted recessives being increased in extent." Castle and Phillips discuss the theory of modifiers but discard it in favor of the effect of selection upon unit characters.

In the main the work of the last decade has supported the pure line hypothesis. As noted above this hypothesis is in full accord with the modern conception of inheritance. For this reason no doubt it has been much more readily accepted than if the reverse were the case. However, the possibility must not be lost sight of that, as has happened in the past, our present conception of the hereditary process may be materially altered in the future. In view of such a possibility it would seem well to make certain of the facts and to study these from various points of view.

The present paper is, in a way, a preliminary report. The selections have been carried on for only three generations. This

[10]MacCurdy, H. and Castle, W. E. Selection and Cross-breeding in Relation to the Inheritance of Coat-pigments and Coat-patterns in Rats and Guinea-pigs. Carnegie Institution of Washington, Publication No. 70, 1907.

time is admittedly very short. However, it has seemed advisable to analyze the results up to this point at the present time and to see if by the use of somewhat different methods new light could be thrown upon these problems. It is proposed to continue certain of these experiments with the object of applying still other methods of analysis to them.

In 1911 there was planned at this Station a series of experiments to test the effect of selection in pure lines of oats. This work has been continued so that now there are available for study the results of three successive selections. The work was originally planned by Dr. Pearl and was carried on under his general direction until the summer of 1913 when, along with other plant breeding work, it was turned over to the writer, (F. M. Surface). Various people have been associated with this work. In 1911 Dr. E. P. Humbert looked after the field work. In 1912 and part of 1913 Dr. M. R. Curtis and Mr. C. W. Barber were in charge of this work.

At the beginning of this work three general lines were planned. First, the attempt to determine the influence of selection when the plants were grown under exceptionally favorable conditions in regard to food material. Second, there was the attempt to determine the influence of selection, if any, upon plants grown under very unfavorable conditions in regard to food supply. Finally it was planned to see whether any permanent effect could be produced within a given pure line by growing it for a period of years under very good or under very poor conditions. It is the purpose of the present paper to deal only with the first of these categories, viz., the effect of selection upon pure lines grown under favorable conditions.

Materials and Methods.

The oat flower is almost always self-fertilized. Rimpau[11] says that in dealing with 19 different varieties of oats during a period of six years he observed only five spontaneous crosses. Our own observations would tend to show even a much smaller number than this. For several years garden rows of different

[11]Rimpau, W. Kreuzungsproduktion landw. Kulturpflanzen. Landw. Jahrb. 1891.

varieties of oats have been grown only one foot apart. At the time of blooming the heads of one row interlock with those of the adjacent rows. Although black, yellow and white oats, open and side heads have been grown next to each other, we have never observed a single natural cross. In no case were all the grains of any one row planted individually the next year, but in many cases a large per cent. of these have been grown. It seems certain that under our conditions, at least, natural crossing is extremely rare in oats.

If this is true it can be shown that practically every oat plant will be homozygous for all of its characters. Thus Jennings[12] has shown that starting with the heterozygotic condition the proportional number of pure homozygotes produced by continued self-fertilization is given by

$$X = \left(\frac{2^n - 1}{2^n}\right)^m$$

where X = the proportional number of pure homozygotes, n = the number of successive self-fertilizations and m = the number of pairs of characters. From this we find that if there are 10 pairs of characters and 10 self-fertilizations, X = 0.97057 or less than three heterozygotes in 100. If there are 20 pairs of characters and 20 self-fertilizations X = 0.999908 or only two heterozygotes in a million individuals.

Since it is extremely probable that the ancestors of any given oat plant have been self-fertilized for many generations, it may be assumed that every oat plant is homozygous for all of its characters unless, indeed, the number of separately inherited characters is very great (several thousand).[13] In this respect the oat plant furnishes excellent material for the study of selection within pure lines.

In 1910 a large number of individual plants were selected from the variety test plots of that year. Each of these plants was harvested and threshed separately. In 1911 the seed from each plant was grown in a single row in the oat garden. Each row contained 25 plants. The seed was planted by hand. The

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[12]Jennings, H. S. The Production of Pure Homozygotic Organisms from Heterozygotes by Self-fertilization. Amer. Nat., Vol. XLVI, pp. 487-491, 1912.

[13]With 1000 characters and 20 self-fertilizations there would be less than 5 heterozygotes in 1000 individuals.

plants were three inches apart in the row and the rows in 1911 and 1912 were alternately one foot and two feet apart. That is, between the first two rows there was a one-foot space; between rows 2 and 3 there was a two-foot space; between rows 3 and 4 a one-foot space and then again a two-foot space. In this way each plant was allowed the same amount of space, viz., 54 square inches, or two and two-thirds plants to each square foot.

As soon as ripe the plants from each row were pulled and tied in bundles bearing a tag with the row number. These bundles were hung in the curing shed until thoroughly dry. Then each plant was threshed separately by hand and various data recorded concerning it. (cf. p. 8).

In most cases not more than 20 plants were threshed from a single row. These were taken entirely at random just as they came from the bundle. In no case were mutilated plants included.

For planting the next year individual plants with exceptionally high or exceptionally low characters were chosen. These were planted in the same kind of garden rows and were harvested and threshed as before. With the exception of one particular the procedure has been the same every year. The one exception is that in 1913 and 1914 the rows were all planted one foot apart instead of alternately one and two feet as used in 1911 and 1912. This change in the method of planting was made through a mistake in 1913. For certain reasons it seemed advisable to continue this method in 1914. This change in the amount of space allotted to each plant undoubtedly affected the absolute yield and other characters of the plants. However it is also found that seasonal variation so affected many of the characters of these plants that it is not possible to deal with the absolute figures from one generation to the next. Instead resort must be had to some measure which eliminates the absolute measurement to a large extent.

It is extremely difficult to get measurable characters of oat plants which are not materially affected by environmental conditions. In order to carry this work along with other problems it was necessary to take characters which could be fairly easily measured or counted. After a careful study of the available characters it was decided to use the more obvious characters

but ones which would certainly be affected by the environment. It is necessary to deal with these data in such a way as to eliminate the effect of changes in the mean absolute value.

The characters chosen for study were (1) the total height from the crown to the tip of the tallest culm, (2) the number of culms which bear seed, (3) the weight of the whole plant including the roots, (4) the weight of the grain, and finally (5) the weight of the straw obtained by difference. All of these characters can be easily and rapidly obtained. One difficulty not clearly foreseen is that each of these characters is highly correlated with each of the other characters, so that, as a matter of fact, the results obtained by selection for any one character will be, to a large extent, duplicated in the case of another character in the same material.

Special progeny record sheets were used for recording the data. One of these sheets is reproduced in facsimile in Fig. 1.

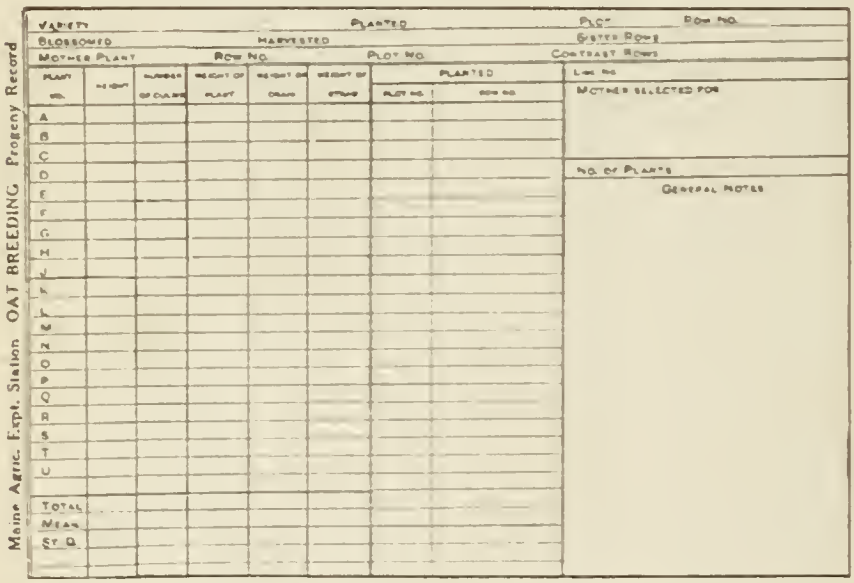

Fig. 1. Facsimile of progeny record blank used in the oat breeding work.

The system of records is such that it is possible to trace the complete pedigree of any individual either backwards or forwards. The system of records in use in the plant breeding work at this Station will be given in some detail in another paper and will not be repeated here.

The labor of threshing each plant separately was found to be so great when several hundred rows were grown that in some cases rows from which we did not expect to breed were threshed as a whole and the average yield per plant obtained as usual. In no case were plants included which were in any way mutilated. On this account the number of plants was sometimes less than 20.

In the following paper all results are based upon the average per plant of the given character for a given row. It is necessary to deal with one character at a time and, as has been mentioned above, all of the characters show essentially the same thing. We will deal first with the weight of grain per plant, or the yield. This character is as satisfactory as any of the others, and it has the advantage that it is of practical importance.

Selection for Yield of Grain.

Out of some 200 pure lines started in 1911, 28 lines representing 13 varieties were chosen for carrying on this selection work. Table 1 gives the line numbers by which they are designated, the variety from which they were selected and the average yield of grain per plant for each of the four years that they have been grown. A description of the varieties from which these lines came has been published in another place.[14] In general these pure lines show the characters typical of the variety from which they were selected. In one or two cases, as line Nos. 104 and 183, these pure lines are quite different from the commercial varieties from which they came. They are probably derived from mixtures of seed in the original varieties.

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[14]Surface, F. M. and Barber, C. W. Studies on Oat Breeding. I. Variety Tests, 1910-1913. Ann. Rept., Me. Agr. Exp. Sta. 1914, pp. 137-192. (Bull. No. 229).

TABLE 1.

Showing the Source, Number of Rows, Number of Plants and Mean Weight of Grain for Each Line for Each Year.

Line No.	Variety.	1911.			1912.			1913.			1914.			Average yield for four years, gms.
		No. rows.	No. plants	Mean yield per plant. gms.	No. rows.	No. plants.	Mean yield per plant. gms.	No. rows.	No. plants.	Mean yield per plant. gms.	No. rows.	No. plants.	Mean yield per plant. gms.	
33	Early Champion	1	19	13.82	4	82	9.32	9	195	5.47	2	36	7.44	*9.01*
44	Imported Scotch	1	20	19.35	4	84	10.50	6	120	7.35	8	162	13.18	*12.60*
57	Senator	1	20	12.65	6	102	9.39	7	135	6.15	10	200	11.02	*9.80*
60	Senator	1	11	16.91	6	106	10.40	12	244	6.29				
74	President	1	18	16.50	4	78	11.00	4	80	4.35	8	139	12.69	*11.14*
82	President	1	20	16.40	4	78	8.34	8	160	5.22	8	171	11.84	*11.20*
104	Swedish Select	1	20	12.00	6	128	10.37	7	140	2.91	7	138	13.39	*9.67*
125	Imported Scotch	1	20	9.98	6	113	9.35	7	141	4.41	8	170	12.29	*8.98*
128	Reg. Swedish Select	1	20	13.10	6	110	8.60	6	120	3.82	7	155	13.55	*9.77*
130	Swedish Select	1	20	13.45	4	81	8.23	6	119	5.23	2	30	12.88	*9.95*
133	Swedish Select	1	20	11.45	4	82	10.43	4	77	3.53	2	33	13.88	*9.82*
139	Reg. Swedish Select	1	20	13.50	8	126	10.12	11	219	6.88	8	174	12.17	*10.74*
152	Swedish Select	1	17	17.00	1	66	10.21	4	78	5.81	2	26	16.42	*12.86*
158	Reg. Swedish Select	1	20	17.50	3	18	13.18	5	119	5.79				*12.16*
183	Prosperity	1	12	23.70	4	81	9.53	5	102	1.68	2	35	15.69	*12.65*
204	Hamlin	1	20	16.30	4	77	13.14	17	367	5.92	2	40	10.82	*11.54*
217	Hamlin	1	20	13.93	9	174	12.71	12	260	4.75	2	40	14.75	*11.53*
238	Reg. Swedish Select	1	20	13.10	8	150	11.27	12	240	6.09	8	145	12.35	*10.70*
250	Imported Scotch	1	19	14.97	1	80	11.13	4	80	5.75	2	35	11.28	*10.78*
262	Victor	1	20	10.45	6	130	6.44	6	120	4.92	12	230	11.95	*8.44*
280	Unnamed White	1	20	11.85	4	85	6.45	4	81	4.40	2	31	14.58	*9.32*
286	Banner	1	20	16.00	18	363	11.35	44	871	4.87	34	716	13.21	*11.36*
307	Banner	1	20	15.27	6	122	12.10	12	242	7.03	19	439	11.54	*11.48*
330	Black Tartarian	1	20	10.43	6	121	4.75	12	252	4.36	2	39	10.85	*7.60*
334	Irish Victor	1	19	15.31	4	87	9.06	4	80	3.94	10	235	13.33	*10.42*
336	Irish Victor	1	20	16.65	4	82	12.14	6	118	4.49	2	39	13.45	*11.68*
337	Irish Victor	1	18	15.78	6	107	9.49	15	312	5.42	8	204	11.65	*10.48*
340	Irish Victor	1	15	17.77	1	87	10.87	9	178	3.71	2	31	15.41	*11.94*
	Total.	28	528	415.15	156	3,030	280.17	258	5,250	140.54	179	3,693	331.61	*287.12*
	Average	1.0		14.89	5.3		10.01	9.0		5.02			12.87	*10.25*

From this table it is to be noted that there is a great difference in the average yield per plant for the same pure line in different years. These differences are due in all probability to differences in external conditions. The highest average yield for all the lines was obtained in 1911. In this year the conditions for the growth of garden plants was very favorable. The lowest yield was obtained in 1913. This was not a good oat year in many respects. However, two things contributed to make this year's yield particularly low. In the first place it has already been noted that the garden rows were planted only a foot apart in 1913, while in the two previous years the average distance between rows had been one and one-half feet. In the second place these garden rows were grown on the same piece of ground for the three years, 1911, 1912 and 1913. Whether soil toxins produced by the same crop in previous years operated to decrease the yield in 1912 and 1913 we are not able to say. At any rate this point should be mentioned as a possible factor. It should further be pointed out that the field plots during these years showed an increase in the average yield for 1913 over the two preceding years.[25]

Only a part of the decrease in the 1913 garden yield can be accounted for on the basis of the different spacing. In 1914 the rows were again planted one foot apart but the garden was moved to another plot of ground. The average yields in 1914 compare very favorably with those of 1911 and 1912. 1914 was an exceptionally good oat year and no doubt the average yield is somewhat better than can be expected for a series of years. However, this shows that conditions other than spacing may greatly influence the yield of garden plants. It is probable that the results as a whole would have been but little more uniform had the spacing been the same in each year.

The number of minus and plus selections has been about the same in each pure line each year. It is true that owing to the skew distributions of the plants about their means the plus selections averaged to deviate somewhat farther from the means than did the minus selections. However, in view of the results obtained in the latter portion of this paper it is not probable that these differences have had any influence upon the mean yields in the later years.

[25]Surface and Barber. *Loc. cit.*

EFFECT OF SELECTION TESTED BY METHOD OF DEVIATIONS.

In view of the fact that external conditions are able to cause such great fluctuations in the mean yield from year to year it is not possible to compare directly the yields of one year with those of the next. In other words selection in the plus direction might very well have produced a marked effect, yet owing to environmental conditions the yield of these plus selections might be lower than the yield of the pure line in the previous year.

Further our pure lines have been selected from a number of different varieties. Many of these varieties show tendencies to yield at different rates. Consequently from such heterogeneous material it would not be possible to compare the direct effect of selection upon yield for all of the pure lines. Thus if we should approach the question by the correlation method and correlate the yield of selected plants with the average yield of the resulting rows we might very well obtain a significant correlation due entirely to the heterogeneity of the material.

For these reasons it is desirable to obtain some measure of the yield which is not so greatly affected by the seasonal fluctuations. The simplest way of doing this is the method of differences. Thus we may determine the mean yield for a pure line in a given year. We may then find the deviation, either plus or minus, of each row from this mean. The sum of all these deviations is of course equal to zero. Similarly we may find the mean of this same pure line in the previous year and then determine the amount and direction of the deviation of the selected plants from this mean. The sum of these latter deviations is not necessarily equal to zero. They are the deviations of a few selected plants from a mean determined from all the plants of that line grown in the same year.

These differences indicate the amount and direction that a given selected plant deviates from the mean of its line and likewise the amount and direction by which its daughter rows deviate from the mean of the same line in the year in which they were grown. Thus, if there is an effect of the selection a plus selection ought, on the average, to result in a row which also deviates in the plus direction.

These differences are to a large extent independent of the absolute size of the mean. They are, of course, dependent

upon the size of the mean in the same sense that a standard deviation is dependent upon the size of the mean. The larger the absolute size of a character the greater are its chances for variation. It would be desirable to determine the standard deviation of each pure line and then divide each deviation by the standard deviation of its line. Thus expressed in terms of the standard deviation these differences would be entirely independent of any differences in the absolute means. However, the number of rows in each line is often entirely too small to determine a reliable standard deviation.

By the use of these differences it is possible to treat all of the data together. Thus so long as each deviation is measured from the mean of its own pure line we can put together the results from all the lines regardless of the variety from which they came.

As a first approach to the question of the influence of selection within the pure line, tables have been formed for each line as follows:

TABLE 2.

Table for One Pure Line Showing the Effect of the 1911 and 1912 Selections upon the Rows Grown in 1913. The Figures within the Table Represent Deviations from the Mean of this Pure Line for the Year Indicated.

LINE NUMBER.	1913 row No.	SELECTED PLANTS. 1911. +	1911. −	1912. +	1912. −	ROWS OF 1913. Selection in 1911 +, 1912 + +	+ −	Selection in 1911 −, 1912 − +	−	Selection in 1911 +, 1912 − +	−	Selection in 1911 −, 1912 + +	−
82	163	11.60	-	15.66	-	-	1.21	-	-	-	-	-	-
	162	11.60	-	10.16	-	2.66	-	-	-	-	-	-	-
	164	11.60	-	-	4.34	-	-	-	-	-	-	-	-
	165	11.60	-	-	5.34	-	-	-	-	-	1.22	-	-
	160	-	6.90	7.66	-	-	-	-	-	0.38	-	-	-
	158	-	6.96	10.66	-	-	-	-	-	-	-	-	0.12
	161	-	6.99	-	3.34	-	-	-	0.22	-	-	-	0.09
	159	-	6.90	-	3.84	-	-	-	0.17	-	-	-	-
Total .		46.40	27.60	44.14	16.86	2.66	1.21		0.39	0.38	1.22		0.21

From this table it is seen, for example, that the first row (No. 163) resulted from a plus selection in 1911 which was 11.6 grams above the mean of that year and from a plus selection of 15.66 gms. in 1912. The average yield of this row itself, however, showed a minus deviation of 1.21 gms. Thus this row deviated in the opposite direction from that for which it had been selected. The next row No. 162 with practically the same kind of selection gave a plus deviation of 2.66 grams.

The first question to arise is whether plus selections have, *on the average,* resulted in rows with a greater plus deviation and likewise whether the minus selections have given an excess of negative deviations. In order to make clear the method of procedure we will first examine the results of the single small line given in Table 2.

In this table is will first be noted that the total plus deviation of the selected plants (1911 and 1912) is in each year considerably in excess of the total minus deviation. As noted above this arises from the skew distribution of the individual plants about their means. The range extends much farther in the plus direction than in the minus and hence allows the selection of larger plus deviations.

From the sums of the columns in the second part of the table (1913 rows) the effect of either the 1911 or the 1912 selection can be determined and likewise the combined effect of two plus or two minus selections. Thus the 1913 rows resulting from plus selections in 1911 show a total plus deviation of 3.04 gms. and a total minus deviation of 2.43 grams. The 1911 minus selections show zero plus deviations and 0.60 minus deviations. Thus the deviations of the 1913 rows show a tendency to follow the line of the 1911 selections. The 1912 plus selections give a total plus deviation of 2.66 gms. and a total minus deviation of 1.42 gms. The 1912 minus selections give 0.38 gms. plus and 1.61 gms. minus, again showing a marked tendency to follow the direction of the selection in 1912. We further note that where the selection has been plus in both years there is an excess of plus deviations and with two minus selections an excess of minus deviations.

Of course the number of rows in this one line is too small to have any significance in itself but it serves to show the method used. It has been pointed out above that by using the

deviations from the means of the respective lines it is possible to lump together all of the pure lines regardless of variety or absolute yield and thus obtain sufficient data upon which to base more definite conclusions.

On account of the lack of space the detailed tables for each pure line will not be given. Instead summary tables showing the effect of the plus or minus selections of each year upon the yield of each of the succeeding years will be given.

It must be remembered that in dealing with these data in the present way two factors are entirely neglected. (1) No account is taken of differences in the size of the deviations of selected plants. All plus deviations whether of 20 grams or one-tenth of a gram are given equal weight and similarly for the minus selections. (2) No account is taken of possible differences in the relative variability of the different pure lines. These two factors will be taken into account in a later section of this paper. It is desirable to consider first the results obtained by the method outlined in the preceding paragraphs.

Table 3 shows the effect of the plus and minus selections made in 1911 upon the rows grown in each of the three succeeding years. Thus the 1912 rows show the immediate effect of the selection. The rows of 1913 and 1914 have each been subjected to other plus and minus selections in the later years. It is to be expected that the results, if any, of the 1911 selection would be somewhat obscured in these latter years. The results of successive plus and of successive minus selections will be discussed in a later paragraph.

Table 4 shows the effect of the 1912 plus and minus selections upon the rows grown in 1913 and 1914. Similarly Table 5 shows the effect of the 1913 selection upon the 1914 rows.

TABLE 3.

Showing the Effect of the 1911 Plus and Minus Selections upon the Rows in Each of the Three Succeeding Years.

Rows grown in		Selected Plants.		Daughter Row.			
				+Selections.		—Selections.	
		+	—	+ Deviations.	— Deviations.	+ Deviations.	— Deviations.
1912	Number of rows	82	74	44	38	33	41
	Total deviation	739.88	437.97	58.42	42.53	37.62	53.33
	Average deviation per row	9.023	5.919	1.328	1.119	1.140	1.301
1913	Number of rows	126	132	53	73	58.5	73.5
	Total deviation	1272.71	821.60	58.38	56.24	54.03	56.19
	Average deviation per row	10.101	6.224	1.102	.770	.924	.765
1914	Number of rows	84	94	38.5	45.5	45	49
	Total deviation	909.88	590.18	50.88	56.84	66.91	61.04
	Average deviation per row	10.832	6.279	1.337	1.249	1.487	1.246

TABLE 4.

Showing the Effect of the 1912 Plus and Minus Selections upon the Rows in Each of the Two Succeeding Years.

Rows grown in		Selected Plants.		Daughter Row.			
				+Selections.		—Selections.	
		+	—	+ Deviations.	— Deviations.	+ Deviations.	— Deviations.
191e	Number of rows	134	124	62.5	71.5	49	75
	Total deviation	1098.80	715.42	64.75	54.49	47.66	57.94
	Average deviation per row	8.200	5.769	1.036	.762	.973	.773
1914	Number of rows	92	86	41	51	42.5	43.5
	Total deviation	857.35	530.80	55.97	61.49	61.82	56.29
	Average deviation per row	9.319	6.172	1.365	1.208	1.455	1.294

TABLE 5.

Showing the Effect of the 1913 Plus and Minus Selections upon the Rows in 1914.

Rows grown in		Selected Plants.		Daughter Row.			
				+Selections.		—Selections.	
		+	—	+ Deviations.	— Deviations.	+ Deviations.	— Deviations.
1914	Number of rows	92	86	41.5	50.5	42	44
	Total deviation	499.83	248.92	59.66	53.96	58.13	63.92
	Average deviation per row	5.433	2.894	1.438	1.069	1.384	1.453

These tables show in the two columns to the left of the double ruling the data regarding the selected plants. The four columns on the right show the data regarding the rows which descended from the selected plants.

By way of example we may note in some detail the data relative to the effect of the 1911 selection upon the 1912 rows. (Table 3, upper part). First, it is seen that in 1912 there were 82 rows grown from plus selections, i. e., from plants whose yield of grain was above the average of their respective pure lines. Likewise there were 74 rows from minus selections. The 82 plus selections showed a total deviation above the means of their lines of 739.88 grams, or an average plus deviation of 9.02 grams per plant. Likewise the 74 minus selections showed a total deviation of 437.97 grams below the respective means, or an average minus deviation of 5.92 grams per plant. In these selections more than one row was frequently grown from the same plant. In such cases the same plant enters into the total deviation as many times as there are rows from it.

Turning to the second part of the table it is seen that of the 82 rows grown from plus selections, 44 showed deviations above the mean of their line and 38 gave deviations in the minus direction. The total deviation of the 44 plus rows was 58.42 grams against 42.53 grams for the 38 minus rows. There is thus a difference of 15.89 grams in favor of the selection. The average deviation per plant for the plus rows is 1.328 grams and for the minus rows 1.119 grams.

Again, of the 74 rows from the minus selections 33 showed plus deviations and 41 minus deviations. The total plus deviations were only 37.62 grams while the total minus deviations were 53.33 grams.[18] In the case of these minus selections the average deviation per plant for the plus rows is 1.140 grams and for the minus rows 1.301 grams.

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[18]Since for all the rows in any one year the sum of the plus deviations must equal the sum of the minus deviations it follows that an excess in either direction in the rows from plus selections must be offset by an equal excess in the opposite direction in the minus selections. Thus the difference between 37.62 and 53.33 is 15.71 grams, practically the same as in the case of the plus selections. In most of the distributions these differences are not exactly equal because the deviations of the rows from their line means were carried to only two places of decimals. The errors are always less than one gram and are neglible.

There is then apparently, a decided effect of the selection made in 1911 upon the plants grown in 1912. As shown in table 3 the apparent effect of the 1911 selection upon the rows of 1913 and 1914 is very much less. The 1914 rows show an excess total deviation in the opposite direction to that of the selection. The average deviation per row shows some differences in the different years. Thus in 1912 the average deviation per row was noticeably greater in the direction of the selection. In both 1913 and 1914 (Table 3) the plus rows resulting from the plus selections show a larger average deviation. However, in the case of the minus selections the minus deviating rows showed a smaller average deviation than the plus rows.

Turning to table 4 it is seen that in the 1913 rows there is again a marked effect of the selection. However in the 1914 rows there is an excess of the total deviation in the opposite direction to that of the selection in 1912. Here there is, in fact, a decrease in the yield of the plus selections over that of the minus selections.

In table 5 it is seen that there is an excess of the deviation, in the direction of the selection.

Considering all three tables it is to be noted that in the year immediately following the selection there is a more or less pronounced effect of the selection as indicated by the total deviations. In each case the plus selections have resulted in a larger total plus deviation of the daughter rows and the minus selections in a larger total minus deviation. The effect of the selection upon the rows grown two and three generations after the selection is very much less marked. In two of the three cases the total deviations show an excess in the opposite direction to that of the selection. These rows have of course been subjected to secondary and tertiary plus and minus selections and it is possible that these latter have outweighed the original selection.

It is also seen that in the year following the selection the average deviation is usually larger in the direction of the selection. The one exception to this is in table 4 in the minus selections grown in 1913. As measured by the average deviation, there does not appear to be a very marked effect of the selection.

STATISTICAL SIGNIFICANCE OF DEVIATIONS.

The question next arises—are any of these deviations in the direction of the selection greater than might be expected in random samples drawn from a similar population? In other words, are these deviations statistically significant?

In the first place it is clear that unless there is some influence of the selection the number of rows showing plus and minus deviations should be the same. This should be true not only of all the rows grown in any one year, but also of the rows from the plus selections and from the minus selections taken separately. From tables 3 to 5 it is seen that in many cases the observed number of rows is not far from the expected. Thus in table 3 for the rows grown in 1912 there are in all 77 rows showing plus deviations and 79 rows showing minus deviations. It can also be shown that in the plus selections or in the minus selections the number of rows does not deviate sensibly from the number expected if there was no influence of the selection.

The same conclusion can be drawn from inspection of the number of rows in each year, except those for 1913 (Tables 3 and 4). In this year there is obviously an excess of rows showing minus deviations. In 1913 there were 111.5 rows showing plus deviations and 146.5 rows showing minus deviations. The expected number is 129 rows in each case. The deviation from the expected is 17.5 rows. The question as to whether such a deviation could arise in random sampling may be determined by comparing the deviation with the standard deviation of simple sampling. The standard deviation of simple sampling is given by

$$S.\ D. = \sqrt{n\ p\ q}$$

In this case $n = 258$, $p = q = \frac{1}{2}$ and

$$S.\ D. = 8.03$$

The actual deviation is just a little over two times the standard deviation and could arise from random sampling. But from tables of the probability integral it is found that in random sampling a deviation as great or greater could be expected only about 2 times in 100 trials. The odds against the occurrence of a deviation as great or greater than this one are about 49 to 1. Thus it is extremely unlikely that the distribution of rows showing plus and minus deviations in 1913 was due to chance alone.

It has already been pointed out that in 1913 the absolute yield of grain was much lower than in any of the other years (Table 1). This was caused by environmental conditions which have been discussed (p. 11). Apparently these conditions caused a larger number of rows to fall below the mean than would ordinarily be the case. It follows that the rows which were above the mean must have shown much larger average deviations than the minus rows. Just why this should occur is not entirely clear. It appears that some rows were not at all or very slightly affected by the adverse conditions, while the majority of rows were much more seriously affected. Perhaps this is due to non-uniformity of the soil. If the decrease was due to soil toxins, these may have been unevenly distributed through the soil.

Attention has already been directed to the fact that the total deviations in the year immediately following the selection show an excess in the direction of the selection. This can be brought out better by putting the figures in the form of percentages. From previous discussion it is clear that we need to deal only with one of the selections, either the plus or the minus. Table 6 shows for the plus selections the percentage of the total deviations falling in the plus rows and in the minus rows.

TABLE 6.

Percentage of Total Deviations for the Plus Selections which Fall in the Plus and the Minus Rows.

Selection made in	Rows grown in	+Selection.	
		+	−
1911	1912	*57.87*	*42.13*
"	1913	50.93	49.07
"	1914	47.24	52.76
1912	1913	*54.30*	*45.70*
"	1914	47.65	52.35
1913	"	*52.51*	*47.49*

This table shows that the only instances in which the deviation can be significantly beyond the expected ratio of 50 per cent. are the rows in the years immediately following the selection (*italics*). Unfortunately if we attempt to determine the probable error of these ratios we get into trouble from the manner in which the sampling was done. Whatever may be the significance of the individual ratios, the fact that the excess is in the same direction and fairly large in each of the three years makes

it probable that, on the whole, some significance may be attached to them.

Before discussing this point further we will examine the relation of the average size of the deviation in the plus and minus rows. These averages are given in tables 3 to 5. Their relation to each other will be made simpler by figure 2.

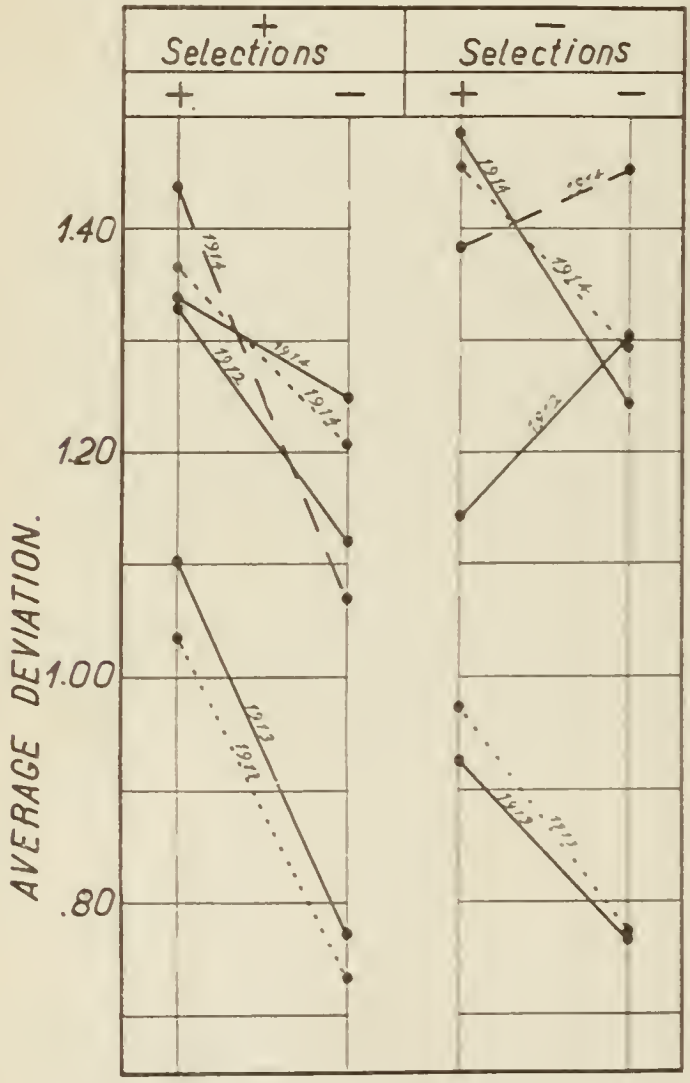

Fig. 2. Showing the average deviation per plant row, in relation to the character of the selection. The years given in the figure are those in which the designated rows were grown.

Selection in 1911 ————————

Selection in 1912 .....

Selection in 1913 —— —— ——

From this figure it is seen:—

1. That in every case the plus selections have shown a larger average deviation in the plus direction.

2. The minus selections on the other hand do not show such a regularity. In only two out of the six cases is there a larger average deviation in the direction of the selection.

3. It is of interest to note that the average deviation per plant row is much smaller in 1913 than in the other two years. It has been pointed out in a previous paragraph that the 1913 yields were much lower than in the other years. It has also been noted that there is an excess of rows showing minus deviations in this year. This latter fact is evidently associated with the fact that in this year the minus selections show a very much larger average deviation in the direction opposite to the selection.

In the 1911 selection and 1912 rows and the 1913 selection and 1914 rows the average deviation in both the plus and minus selections is in the direction of the selection. It will be further noted that these are rows grown the next year after the selection. The question arises as to whether in these years the deviations are greater than might be expected in random sampling. This question can perhaps be tested easiest by determining the goodness of fit of the expected and observed average deviations.

Slutsky[17] has recently extended Pearson's tests for the goodness of fit to include other types of curves than frequency distributions. It is possible to apply this method to the present data and determine from Elderton's tables the probability that our observed deviations could have arisen from random sampling. The data for the 1911 selection and 1912 rows have been chosen for this purpose since these rows show the most consistent deviations in the direction of the selection. The theoretical points are determined by considering that if there were no effect of selection the average deviation of the rows from plus selections would be equal in the plus and the minus directions. The same would be true of the minus selections. The test is then made to

[17]Slutsky, E. On the Criterion of Goodness of Fit of the Regression lines and on the Best Method of Fitting Them to the Data. Jour. Roy. Stat. Soc., Vol. LXXVII, Pt. 1, pp. 78-84. See also, Pearl, R. Amer. Nat. Vol. 48, pp. 505-507, August, 1914.

determine whether these four points deviate farther from the theoretical values than could be expected. By this test we find that

$$P = .6561$$

Or, in other words, if there is no effect of selection we should expect to get a fit as bad or worse than that observed in 65 out of every 100 trials. This is a reasonably good fit and we may conclude that these deviations do not behave differently than might be expected if there was no effect of the selection. There is thus no positive evidence that the selection has produced any effect even in the first year after the selection.

SUMMARY.

Summarizing the results of this section it may be said that from the data so far examined there is some evidence of an effect of a selection upon the rows grown the next year. In no single case is the effect great enough to be significant in itself. However, the fact that there is a reasonably large difference in the same direction after each of the three selections indicates that there may be some immediate effect of the selection.

It is quite possible that the apparent effect of selection upon the rows grown the following year is to be explained as physiological rather than genetic. It is possible that the larger and consequently more vigorous plants produce grain which has more nourishment or which for some other reason gives the new plant a better start. This brings us to an old queston which it is extremely difficult to answer. It will be considered in a later paragraph.

The Effect of Successive Selections in the Same Direction.

If the slight effect of selection upon the following generation, as noted above, is due to changes in the germinal substance, then a much more marked effect ought to be produced by two or three successive selections in the same direction. A portion of the 1913 rows have been subjected to two such selections and some of the 1914 rows to three such selections. The results are shown in table 7.

TABLE 7.

Showing the Effect of Two or Three Successive Selections in the Same Direction.

	1913 Rows.				1914 Rows.			
	++ Selection.		- - Selection.		+++ Selection.		- - - Selection.	
	+	—	+	—	+	—	+	—
Number of rows	28	39	24	41	17	23	17	21
Total deviations	26.93	28.75	16.21	30.45	20.01	30.07	19.60	36.66
Average deviation per row	.962	.737	.675	.743	1.177	1.307	1.153	1.746

From this table it is noted:

1. That with two successive plus selections (1913 rows) there is no effect of the selection. There is a slight excess of the total minus deviations, i. e. in the direction opposite to the selection.

2. With two successive minus selections (1913 rows) there is a substantial excess of the total minus deviations. The total minus deviations are almost twice the total plus deviations.

3. With three successive selections in the same direction (1914 rows) there is an excess of the minus deviations in each case. Even where the selection has been plus in each year the total minus deviation is one-third greater than the plus deviations. Here there is a substantial excess in the opposite direction to the selection.

4. With three successive minus selections there is a marked excess in the direction of the selection.

Judging from these figures it would appear that successive plus selections have resulted in rows which on the average were below the means of their lines. On the other hand successive minus selections have shown in each case very marked excess in the direction of the selection.

The results so far obtained are to a large extent contradictory. It has been seen that, considering the effect of each selection on the years following it, there is some evidence of a positive effect on the year immediately following. If this effect were really due to the selection, then successive selections in the same direction ought to produce a still more pronounced effect. From table 7 it is seen that this prediction is realized in the case of the

minus selections but with the plus selections the opposite result is obtained.

In view of the possible significance of these figures and those exhibited in tables 3 to 6 it is worth while to attempt an analysis of these data by still other methods.

Indices of Selection.

Attention has been called to the fact that in the method used in the preceding pages two factors have been left out of account. These are (1) the possible difference in the variability of different pure lines, and (2) the size of the deviation of the selected plants. That is, all plus deviations of the selected plants have been given equal weight although some plants were 20 grams above the mean and others only a fraction of a gram. If there is any real influence of the selection, a plant 20 grams above its mean should have more effect on the next generation than a plant only one-half gram above its mean. In view of the fact that the results obtained by the preceding method are somewhat doubtful in meaning it will be well to take these factors into consideration.

The difference in the variability of the different pure lines could best be expressed by their standard deviations or coefficients of variation. It would then be possible to divide the deviation of each selected plant or of each row by the standard deviation of the corresponding pure line. This would express the variability of the plant (or row) in terms of the variability of the pure line. However, in the majority of the pure lines used in this work the number of rows is too small to obtain a reliable standard deviation.

Very probably the chief factor in increasing or decreasing the standard deviation of a given line is the size of the mean. The greater the size of the mean the greater the chance for absolute variation. Consequently if each deviation is expressed as a percentage of its mean it is probable that the chief element in the difference in variability will have been taken into account.

We have, therefore, gone through the tables (cf. table 2) for each pure line and expressed the deviation of each plant and each row as a per cent. of the mean of that pure line for the given year.

In order to take account of the second factor, viz. the size of the deviation of the selected plant, the following points may be considered. If there is an effect of the selection the rows from the plus selections will tend to deviate in the plus direction, and *vice versa*. Owing to the regression the deviation of the daughter rows will not usually be so great as that of the mother plant. The amount of this regression and likewise the amount and direction of the deviation of each row in relation to its mother plant may be expressed as an index. If we let *Dm* be the deviation of the mother plant from its mean and *Dd* the deviation of the corresponding daughter row from its mean. then an index, *I*, may be calculated in which

$$I = \frac{Dm - Dd}{Dm}$$

If in this index the daughter row lies at the mean of the pure line, then *Dd* is zero and $I = 1.0$. In this case there is no effect of the selection. If the deviation of the daughter row *Dd* is in the same direction as the deviation of the mother plant, then $I < 1.0$ and there is apparently an effect of the selection. If, on the other hand, the daughter row deviates in the opposite direction to that of its mother plant, then $I > 1.0$.

This "Index of Selection"[18] in reality expresses the amount of regression of the offspring on the parent in the individual case.[19] It also brings together considerable other information into a single constant. Thus if the index is less than 1 we know at once that the row in question deviated in the direction of the selection. It likewise tells us the amount of deviation relative to the selection. If the index is 0.5 the row deviated half as far as the selected plant. If the index is 1.33 we know that the row deviated in the opposite direction to that of the

[18]To be distinguished from a "Selection Index." Cf. Pearl R. and Surface, F. M.—Selection Index Numbers and Their Use in Breeding. Amer. Nat., Vol. XLIII, pp. 385-400, 1909. Also Pearl, R.—Further Notes Regarding Selection Index Numbers, Amer. Nat., Vol. XLVI, pp. 302-307, 1912.

[19]It should be remembered, however, that these indices are not the same as Pearson's coefficients of regression calculated from the correlation coefficient and the standard deviations.

selected plant and that its deviation in that direction was equal to one-third the deviation of the mother plant.

Attention should also be called to the fact that if the deviation of the daughter row is in the same direction and greater than the deviation of the selected plant the index will be negative. Further if the deviation of the daughter row is in the opposite direction and greater than the deviation of the mother plant the index will have a value greater than 2.

These indices may be treated as other statistical constants. Thus, if there is no effect of selection within the pure line these indices, *on the average*, will be equal to 1.0 within the limits of chance deviations. If there is an effect of the selection the average index will be significantly less than 1.0. On the other hand, if the average index is significantly greater than 1.0 it will indicate that there is a tendency for the deviation to swing in the direction opposite to the selection.

In calculating these indices the deviations of the plants and the rows expressed as percentages of their means have been used instead of the absolute deviations. In this way these indices take account of both the factors discussed at the beginning of this section.

Indices have been calculated to show the effect of each of the three selections upon the rows grown in each of the succeeding years. The average index for both the plus and minus selections and for all the rows grown in each year is given in Table 8. Probable errors for the mean index have been calculated from the distributions of all the indices for each year.

TABLE 8.

Showing the Mean Index of Selection for the Plus and Minus Selections and for All the Rows, for Each Year.

Selection Made in	Rows grown in	Mean Index.		
		+ selections.	— selections.	All selections.
1911...	1912	1.1575	1.1556	1.1566 ± .1442
1911.	1913	1.3051	0.8910	1.0932 ± .1522
1911..	1914	1.0053	0.8532	0.9250 ± .0491
1912..	1913	0.9509	0.9615	0.9568 ± .0241
1912..	1914	1.0151	1.0100	1.0126 ± .0139
1913..	1914	1.0285	1.0102	1.0197 ± .0221

From this table it is seen:

1. That in the majority of cases the mean index is not far from the theoretical value 1. From the indices for all the selections in each year (last column) it is seen that in the majority of cases the deviation from 1 is not at all or very little greater than the probable error. In two cases, viz. the 1911 selection and 1914 rows, and the 1912 selection and 1913 rows the difference is very nearly twice the probable error. In these cases the mean index is less than 1 indicating a possible effect of the selection.

2. There is considerable difference in the mean index of the different years. Thus the 1911 selection and 1912 rows show a mean index considerably above 1. However, the probable error of the index for all the selections is practically as large as the deviation of the index above 1. On the other hand the 1912 selections and 1913 rows show a mean index consistently less than 1.0. The difference between 1.0 and the mean index of all the selections is .0432, a little less than twice the probable error. In none of these cases is the deviation from 1.0 statistically significant.

3. On the whole the mean index of the plus selection is greater than that of the minus selection. In only one case (1912 selection and 1913 rows) is this relation reversed. In three of the other years the difference is only nominal. However, in two cases (1911 selection and rows of 1913 and of 1914) the excess of the mean index of the plus over that of the minus selections is quite marked. If we average the six mean indices of the plus selections it is found to be 1.0770, while the corresponding average for the minus selections is only 0.9803. It is very doubtful whether this difference has any significance.

4. There is no evidence from these indices that the selection is more effective upon rows grown the year after the selection than upon rows grown in later years.

Many of the irregularities in these mean indices are attributable to the effect of one or two selections. For example, in Line No. 262 a plant was selected in 1911 whose yield was only 0.05 of a gram above the mean. It so happened that several of the rows grown from this plant deviated from their mean much farther than 0.05. Consequently they gave indices much

greater than 1; in one case an index of —23.5 and in another +48.8. These extreme variations tend to balance each other and no doubt would do so if sufficient rows were grown. But with a small number of rows such a selection may materially change the value of the mean index. There is *a priori* no reason why such small selections should be omitted. For on the selection theory a small variation *should* result in a much smaller deviation in the daughter row. However, there are very few of these small selections in the present data.

In order to show the effect of this one small deviation, which is by far the smallest one in these data, we may give the mean index for the 1911 selection upon the 1912 and 1913 rows when Line 262 is omitted entirely.[20]

TABLE 9.

Mean Index with Line 262 Omitted.

Rows Grown in	Mean Index.		
	+selections.	—selections.	All selections.
1912	0.9952	1.1723	1.0842
1913	1.1249	0.8910	1.0043

Comparing these figures with those in the first two rows of Table 8 it is seen that omitting the effect of this very small selection results on the average in bringing the mean index nearer to 1.

On the whole these indices do not give us any evidence that the selections have had any effect upon the succeeding generations. The values tend to fluctuate about 1.0 as demanded by Johannsen's theory. It should be pointed out that if regression took place within these pure lines according to the Galton-Pearson theory of ancestral inheritance the value of these indices should approach the value 0.333. There is not the slightest indication that they do this.

[20]There were no rows grown from this small selection in 1914.

INDICES OF SUCCESSIVE SELECTIONS IN THE SAME DIRECTION.

As a matter of completeness it will be well to examine the indices for those rows which have been subjected to several successive selections in the same or different directions.

Table 10 shows the mean indices for the four classes of selection possible in the 1913 rows. Table 11 shows the mean indices for the possible kinds of selections to which the 1914 rows have been subjected.

TABLE 10.

Mean Indices of Selection for Each of the Four Kinds of Selection for the 1913 Rows.

Character of the selection.	Number of rows.	Mean Index.		Mean Index Omitting Line No. 262.	
		1911 selection.	1912 selection.	Number of rows.	1911 selection.
++	67	0.7350	0.9252	65	1.1044
−−	65	0.8097	0.8615	64	0.8241
+−	59	1.9525	1.0716	57	1.1481
−+	67	0.9698	0.9766	66	0.9698

TABLE 11.

Mean Indices of Selection for Each of the Possible Kinds of Selection for the 1914 Rows.

Character of Selection.	Number of rows.	Mean Index.		
		1911 selection.	1912 selection.	1913 selection.
+++	40	0.9734	1.0453	1.0821
++−	26	1.0833	1.0128	0.9546
−++	16	1.1394	1.0320	1.0051
+−+	6	0.5460	1.0731	0.9776
+−−	12	1.0912	1.0574	1.3085
−+−	10	1.2460	0.7777	1.1770
−−+	30	0.7536	1.0576	0.9797
−−−	38	0.7335	0.9726	0.9063

From Table 10 it is seen that the apparent marked effect of the two plus selections in 1911 entirely disappears, if we omit Line No. 262 in which there is one selection only very slightly above the mean. In a similar manner the very large mean index for the + selection in 1911 is reduced to a figure comparable with other indices. However, with two minus selec-

tions there is in each case a very marked decrease in the mean index. This index is of the same order of magnitude with each of the two selections. Further it is not essentially changed by omitting the one disturbing line (No. 262) from the 1911 selections.

From table 11 it is seen that there is very little regularity in the indices of the three selections. Thus with three plus selections the mean index shows a tendency to lie slightly above 1, although probably not significantly. At least it may be said that there is no evidence that three successive plus selections have modified these pure lines in the direction of the selection.

With three minus selections the case is somewhat different. With each of the three selections the mean index is considerably less than 1, indicating that possibly the minus selections have produced a real effect upon the pure lines. On going through the individual indices it appears that the result is not due to a few very small indices but that there is a real tendency for the indices in these classes to be less than 1. This result it will be remembered falls into line with the conclusions drawn from Tables 7, 8 and 10.

Selection for Characters other than Yield.

In the preceding pages the only data dealt with have been those for the yield of grain per plant. In order to see whether the other characters upon which we have data behave in a similar manner the records of some of these have been at least partially analyzed. The characters to which most attention has been paid are the height of plant and the number of culms. These show but very little that is essentially different from the data for yield of grain. On this account we will discuss the data for height very briefly and omit the remaining characters.

Tables 12, 13 and 14 show the same data for height of plant that Tables 3, 4 and 5 show for weight of grain.

TABLE 12.

Effect of the 1911 Selections for Height of Plant upon the Rows in Each of the Three Succeeding Years.

Rows grown in		Selected Plants.		Daughter Row.			
				+Selections.		—Selections.	
		+	—	+	—	+	—
1912	Number of rows	86	70	44	42	35	35
	Total deviations	393.35	420.53	180.65	166.00	121.77	136.39
	Average deviation	4.574	6.008	4.105	3.952	3.478	3.897
1913	Number of rows	130	126	61	69	71	55
	Total deviations	566.58	697.39	277.19	267.83	249.56	258.50
	Average deviation	4.356	5.535	4.544	3.882	3.515	4.700
1914	Number of rows	76	102	34	42	52	50
	Total deviations	335.07	726.39	117.45	125.67	194.54	186.31
	Average deviation	4.409	7.121	3.454	2.991	3.741	3.726

TABLE 13.

Effect of the 1912 Selection for Height of Plant upon the Rows in Each of the Two Succeeding Years.

Rows grown in		Selected Plants.		Daughter Rows.			
				+Selection.		—Selection.	
		+	—	+	—	+	—
1913	Number of rows	101	155	55	46	77	78
	Total deviations	540.48	1697.42	179.56	176.09	347.19	350.24
	Average deviation	5.351	10.948	3.265	3.828	4.509	4.490
1914	Number of rows	78	100	40	38	46	54
	Total deviation	401.45	1123.88	139.58	99.27	172.41	212.71
	Average deviation	5.147	11.239	3.490	2.612	3.748	3.939

TABLE 14.

Effect of 1913 Selection for Height of Plant upon the Rows Grown the Next Year.

Rows grown in		Selected Plants.		Daughter Rows.			
				+Selection.		—Selection.	
		+	—	+	—	+	—
1914	Number of rows	101	77	47	54	39	38
	Total deviations	899.73	933.82	169.60	171.11	142.39	140.87
	Average deviation	8.908	12.128	3.609	3.169	3.651	3.707

Inspection of these tables shows:

1. That in each year the number of daughter rows is very equally divided between the plus and minus columns. In no case is the difference greater than might be expected in random sampling.

2. The total deviations of the daughter rows are in most cases also very equally divided between the plus and minus directions. In four out of the six cases the excess of the total deviation is in the direction of the selection. In only one instance is this deviation large enough to be significant. This is in Table 13, the rows grown in 1914. For the plus selection in this year the theoretical total deviation is 119.43 centimeters. The difference between the observed and expected ratios is 20.15 centimeters. As noted before it is difficult to determine the standard error of these total deviations. However, it is probable that this difference is not beyond the range of the fluctuation of random sampling. In all of the other years the difference is certainly insignificant. For this and other reasons noted below, it seems probable that this one large deviation is not significant in connection with the selection.

3. Inspection also shows that the average deviation per plant row is very equally distributed between the plus and minus columns. The largest difference between the observed and expected average deviation is only a little over 0.4 cm. However, in 9 out of 12, or in 75 per cent. of the possible cases the excess is in the direction of the selection. This difference is not greater than might arise in random sampling.

4. There is no evidence that the selection for height of plant has produced a greater effect the first year after the selection than in later years.

Since the above tables do not give any positive evidence of selection, it has not been thought necessary to calculate all of the indices of selection for this character. The indices for two years have been calculated and they show essentially the same thing as the indices for weight of grain. The indices for height tend to vary a little more widely from the average value of 1 than those for grain weight. This is due to the fact that some of the selections for height were much nearer the mean than in the former case. It is not thought necessary to table these indices.

Discussion.

The statistical analysis of these data has given but very little evidence of the positive effect of selection within these pure lines. The one or two instances in which there is some doubt, may be discussed briefly. The first instance is that shown in Table 7 in which the total deviations of the daughter rows show a positive excess in the year following the selection. There is some question as to whether these excesses in the direction of the selection are not to be regarded as coincidences of random sampling. This is rendered more probable because the later analysis by means of the indices show very little evidence for such an effect.

However, if these excesses are to be regarded as significant it is very probable that they are due to physiological rather than genetic causes. It is quite conceivable that the grain from the more vigorous heavy yielding plants differs from that of the smaller plants in either the amount or quality of its food material. It was thought that possibly some evidence on this point could be obtained by determining the correlation between the yield and the weight per 100 grains of individual plants. This correlation was determined for several pure lines but in each case it was significantly zero, even showing a slight negative value in some instances. Thus it appears that the size of the grain is not the determining factor in these data at least. Whether the grain from the large and small plants vary in the character of their nutrient material is a question that we have not studied.

It was pointed out in connection with Tables 7, 10 and 11 that with successive minus selections there was a positive effect of the selection. This was shown both by a study of the deviations from the mean and of the indices. On the other hand, successive plus selections appeared to show a negative effect of the selections. Whether any significance is to be attached to these slight differences or not cannot be decided by the present data.

On the whole these results certainly show that selection within these pure lines of oats has been without any marked effect upon the progeny so far as the characters studied are concerned. The results based upon the study of the indices agrees as closely as could be expected with Johannsen's theory.

It is proposed to continue the selections within certain of these pure lines upon a somewhat different plan. It is hoped that by these methods it will be possible to analyze the data by an individual rather than a statistical method. Such an analysis was attempted with the present figures, but it was found that they are inadequate for that purpose. It is believed that possibly some new evidence can be brought to bear upon the selection question in that manner.

Summary.

The chief points brought out in this paper may be summarized as follows:

1. The present study attempts to analyze the results of three successive years of selection within pure lines of oats. Twenty-eight pure lines representing 13 varieties have been used in this work. In the four years 621 garden rows have been grown involving over 12,500 plants. The characters studied were weight of grain, weight of plant and of straw, height of plant and the number of culms. Only two characters, yield of grain and height of plant, are analyzed in detail in this paper. The remaining characters show essentially the same things.

2. It is pointed out that the oat flower is practically always self-fertilized. It is shown that if this is true every oat plant must be regarded as homozygous for all of its characters. Consequently the oat plant fulfills all the requirements in the original definition of a pure line.

3. The characters studied are subject to rather wide fluctuations due to environment. For this reason it is not possible to compare the absolute values of these characters from year to year. Instead the deviations of the plants and rows from the mean of their pure line in the given year have been used.

4. As a first approach to the problem in hand we have determined the number of rows, grown from plus selections, which deviated in the plus direction and likewise the number deviating in the minus direction. The same thing has been done for rows grown from minus selected plants. Thus for each selection there are four classes of rows. (Cf. Tables 3, 4 and 5). Also the sum of the deviations of the rows in each class has been determined and likewise the average deviation in each class.

5. From these data for the yield of grain, it is pointed out that usually in the year next following a given selection there is an excess deviation in the direction of the selection. This appar-

ent effect of a given selection is very much less noticeable or not at all in the later years. It is probable that the effect in the first year is due to physiological rather than genetic causes.

6. Considering the effect of two and of three successive selections in the plus direction it is seen that there is an excess deviation in the direction opposite to the selection. However, with two and three selections in the minus direction there is an excess in the direction of the selection (Table 7). These results balance each other so that it appears safe to conclude that neither were due to the effect of the selection.

7. The methods of analysis described above leaves out of account two factors, viz. the difference in the variability of the different pure lines and second the size of the deviation of the selected plant. The first of these factors can be partially taken into account by expressing each deviation as a percent. of its mean. The second factor can be accounted for by expressing the deviation of each plant as an index.

$$I = \frac{Dm - Dd}{Dm}$$

where *Dm* is the deviation of the mother plant from its mean and *Dd* is the deviation of the daughter row from its mean. If there is no effect of the selection as Johannsen claims then this index should on the average equal 1. If regression takes place within these pure lines as claimed by the Galton-Pearson theory of ancestral heredity, the index would on the average approach 0.33. In general if the index is significantly less than 1 it indicates some effect of the selection.

8. For the yield of grain, these indices have been calculated for the effect of each selection upon the rows grown in each of the following years. The average index for each class of selection and for all the selections are given in Table 8. As shown in their probable errors these mean indices are not significantly different from 1. This indicates that there is no effect of the selections within these pure lines.

9. The mean indices showing the effect of two or three successive selections in the same or in different directions are shown in Table 10 and 11. These indices are also significantly equal to 1 with the possible exception of the successive minus selections. These later indices are consistently less than 1. Whether they really indicate an effect of the selections or not, cannot be determined from the present data. The values are not very far below 1 and in view of the other evidence we are inclined to regard them as random fluctuations.

10. It is pointed out that where selections are made which are only slightly above or below the mean of their pure line, spurious values of this Index are sometimes obtained. This is especially true if a relatively small number of rows are grown from such a selection. The reason for this is that the means of some rows may deviate much farther from the mean of the line than did the mother plant. This will produce indices very large either positive or negative. *A priori* there is no reason for excluding such small selections. They ought, on the selection theory, to result in rows which would deviate less from the mean of the line than rows grown from large selections. Only one such "small" selection is included in the present data. The effect of omitting the line (No. 262) to which it belongs is shown in tables 9 and 10.

11. The analysis of the selections for height of plant shows essentially the same results as found for yield of grain. Analysis by the method of deviations shows that in only one instance is the excess in the direction of the selection large enough to have any possible significance. For reasons discussed in the text it is probable that this one large deviation is not significant in connection with the selection.

12. Indices of selection for height of plant have been calculated for several of the selections. Since they show nothing essentially different from those for yield they have not been included in the present paper.

13. On the whole the results obtained in this study give no evidence that selection for three years has modified any of the characters studied. The one or two apparent exceptions discussed in the paper might very easily arise in chance distributions where so small a number of years are considered. The weight of the evidence against an effect of selection far outweighs the evidence for such an effect. *It must be concluded that in the present material and for the characters studied, selection for three years has produced no effect which can be detected by the methods used.*

14. It is proposed to continue a portion of these selections and later to attempt an individual analysis rather than the statistical one presented in this paper.